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Offspring dispersal ability covaries with nest-site choice

David M. Delaney
Iowa State University, dmdelane@iastate.edu

Fredric J. Janzen
Iowa State University, fjanzen@iastate.edu

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Offspring dispersal ability covaries with nest-site choice

Running header: Dispersal ability covaries with nest-site choice

David M. Delaney[1,2] and Fredric J. Janzen[1]

[1]Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, Iowa, USA

[2]e-mail: dmdelane@iastate.edu, phone: 217-343-7764

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Data Accessibility

Analyses reported in this article can be reproduced using the data provided by Delaney and Janzen (2018).

Abstract

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INTRODUCTION

Mothers increase their fitness by investing resources in offspring (Trivers 1972). However, resource limitation or conflicting pressures may generate maternal investment tradeoffs (Stearns 1989, 1992; Roff 1992; Balme et al. 2017; Wiernasz and Cole 2018). The optima of such tradeoffs can shift depending upon environmental context (e.g., predation risk, Ghalambor and Martin 2001; Fontaine and Martin 2006; Taborsky 2006; Segers and Taborsky 2011; social setting, Russell et al. 2007; Taborsky et al. 2007) or female traits (e.g., body condition or age; Monaghan et al. 1998; Velando et al. 2006; Kindsvater et al. 2010; Arnold et al. 2018). Yet, optimal investment may also depend upon offspring phenotype. For example, various animals differentially invest in sons versus daughters because parents can increase their fitness by investing in the sex with the greatest return (e.g., Altmann and Samuels 1992; Olsson and Shine 2001; Spelt and Pichegru 2017). Although offspring phenotype can affect post-natal food provisioning in birds and mammals (Magrath 1990; Price and Ydenberg 1995; Wells 2003; Middleton et al. 2007; Soley et al. 2011; Merkling et al. 2014), the role of offspring phenotype on pre-natal investment is less understood (but see offspring size vs number tradeoffs, Smith and Fretwell 1974; Einum and Fleming 2000; Janzen and Warner 2009). In addition, whether offspring performance traits might influence maternal investment strategies is unknown (sensu Sinervo 1990).

For oviparous animals, the location that mothers choose to nest is often the greatest determinant of early-life success for offspring (Bernardo 1996; Resetarits 1996).

For example, nest-site choice can influence offspring phenotype (Janzen 1994; Shine et al. 1997), predation risk (Spencer and Thompson 2003; Forstmeier and Weiss 2004), and proximity to suitable juvenile habitat (reviewed in Refsnider and Janzen 2010). Although environmental conditions and female traits influence nest-site choice, few studies have examined if females choose nest sites that are specifically tailored for the phenotypes of their offspring. Moreover, the few tests of adaptive nest-site choice as a function of offspring phenotype found that females selected nest sites that were as equally beneficial for other offspring as their own (Shine et al. 1997; Mitchell et al. 2013). Nevertheless, offspring phenotype and nest-site choice may still covary if adaptive. For example, embryos that develop into good dispersers could be deposited farther from juvenile habitat if doing so is advantageous (e.g., reduce predation risk of nest). In contrast, embryos that develop into poor dispersing offspring could constrain females to nest closer to juvenile habitat and experience elevated nest predation risk. Thus, while rare, studies that consider the potential impact of offspring phenotype on nest-site choice may reveal an important influence on fundamental investment behavior.

Freshwater turtles are well suited to address this major conceptual issue in behavioral ecology. The survival of terrestrial nests increases with distance to water, because nest predators (e.g., raccoons) often forage along environmental edges (Temple 1987; Kolbe and Janzen 2002a; Spencer 2002; Marchand and Litvaitis 2004; Strickland et al. 2010). However, offspring from eggs deposited farther inland must migrate a greater distance to water upon emergence from their nests. Thus, females may balance a tradeoff between nesting far from water to increase nest survival with nesting close to

water to reduce offspring dispersal distance. Furthermore, mortality during these early life stages is high in aquatic turtles (e.g., *Chelydra serpentina,* 41.1% Janzen 1993; 33–41% Congdon et al. 1999; 37.1% Kolbe and Janzen 2001; *Chrysemys picta*, 25% Tucker 2000, 22% Mitchell et al. 2013; *Trachemys scripta*, 66% Janzen et al. 2000a; 65.1% Janzen et al. 2000b; 42.9% Tucker 2000; reviewed in Iverson 1991), suggesting selection on maternal investment strategies is considerable. Indeed, selection often favors larger hatchlings during dispersal to water (Janzen 1993; Tucker 2000; Janzen et al. 2000a, 2000b; Janzen et al. 2007; Paitz et al. 2007). This trend likely results from survival declining the longer hatchlings spend dispersing (Janzen et al. 2007) and larger offspring dispersing faster (Janzen et al. 2000a, 2000b; Paitz et al. 2007). In addition, older and larger females oviposit larger eggs (Congdon and Gibbons 1985; Congdon et al. 1987; Bowden et al. 2004) and do so farther from water (Harms et al. 2005). Thus, females that oviposit larger eggs may do so farther from water because their larger offspring are capable of longer dispersal (Fig. 1A) and predation on nests decreases with distance from water (Fig. 1B).

To assess the role of offspring dispersal ability in maternal investment strategies, we conducted a dispersal experiment with 428 hatchling common snapping turtles (*Chelydra serpentina*) from 15 nests. We released hatchlings at three distances from water typical of natural nests and subsequently monitored survival and time to disperse during overland dispersal. We predicted larger hatchlings would have higher survival and disperse faster than smaller hatchlings. Furthermore, we predicted these effects would be stronger when offspring were required to disperse farther to water (Fig. 1A). Prior to

collection for the dispersal experiment, we also measured how far nests were naturally constructed from water. Because females may tailor nesting strategy to their young's dispersal ability, we predicted offspring from natural nests located farther from water would have better dispersal performance in our experiment than offspring from nests closer to shore.

METHODS

We monitored the nesting behavior of 16 *C. serpentina* at the Thomson Sand Prairie along the Mississippi River in Illinois from 26 May to 3 June 2017. After a nesting event concluded, we measured the distance between the nest and the River with a GPS (down to ± 2.4 m accuracy, Garmin eTrex 20). We then excavated eggs (n = 16–85 per nest) and moved them to an artificial nest block protected with wire mesh until hatching. No eggs were damaged during this excavation and burial process. Moreover, predation on natural, unprotected nests is high at this site (65%, Kolbe and Janzen 2002b), yet we only lost 1 nest (6%) to predation in our protected nest block. Within the nest block, we placed each clutch about 21 cm deep (near the average depth (~18 cm) and within the range (up to 21.5 cm) at our site; Kolbe and Janzen 2002b; Telemeco et al. 2016) and 0.5 m from the nearest other artificial nest. Incubation in this common-garden arrangement in the field reduced variation in incubation environments among clutches while still exposing embryos to natural abiotic conditions in a location often used for nesting. We placed iButton data loggers in the middle (~16-cm deep) of three nests to monitor thermal conditions in the artificial nest block. We analyzed nest temperatures from the day the

last clutch was placed in the nest block (7 June) to the day of first emergence from a nest (31 July), which represents 77–90% of the entire developmental period of experimental nests.

We encircled nests with 15-cm high PVC on 25 July and monitored nests twice daily for hatchling emergence. The PVC contained emerging turtles from a nest, enabling us to assign clutch to each hatchling. After emergence, we weighed hatchlings to the nearest 0.01 g and measured straight carapace length (SCL) to the nearest 0.01 mm. We notched either the left or right 11th marginal scute and photographed the plastrons to uniquely identify hatchlings upon recapture. The marginal scute mark allowed us to verify that a recaptured hatchling was from our experimental release and reduced the number of photographs we needed to survey by half (sensu Janzen 1993). We housed hatchlings at the clutch level in covered plastic containers (up to 30 hatchlings per container; container size = 23 cm x 35 cm x 9 cm) placed in a large cooler (mean = 4.4 ± 2.22 SD, range = 2–9 days), which we kept in the shade at the field site to reduce metabolic activity until enough hatchlings emerged for the dispersal experiment to begin. We monitored captive hatchlings at least twice daily to verify adequate thermal and moisture conditions. We observed no aggression among hatchlings and provided no food, but sprayed clean water into each container daily. No hatchlings died in captivity, and length of time in captivity did not affect post-release survival ($F_{1, 412} = 0.92$; $P = 0.3373$), suggesting our processing and housing methodology did not adversely affect hatchlings.

We constructed a straight 250 m drift fence that paralleled the Mississippi River and buried 4.5-liter plastic jars every 5 m to capture hatchlings as they dispersed from

their terrestrial release locations to water (Fig. S1; sensu Janzen 1993; Congdon et al. 1999; Kolbe and Janzen 2001). We randomly divided up to 30 hatchlings/clutch into six groups and released them at either 25, 62.5, or 100 m from the fence. Each release distance was spatially replicated twice so that each release distance had between 69 and 73 dispersers (total N = 428), which falls within the natural clutch size range of *C. serpentina* (Iverson et al. 1997; Kolbe and Janzen 2001; Ernst and Lovich 2009). Thus, there were two groups of release points (i.e., a North and a South replicate) with a release point for each distance from water. On 8 August, we excavated 15 cm pits at each release point to simulate natural nests, inserted hatchlings into the pits, and placed upturned 19-liter buckets over the release points. We allowed hatchlings to acclimate for 15 minutes and then used 10 m long ropes to remove buckets to reduce disturbance by observer presence. Peak nest emergence of *C. serpentina* occurs from 1000–1100 h in Michigan (Congdon et al. 1999), and most terrestrial movement occurs after sunrise and before 1300 h at our study site (Janzen 1993; Kolbe and Janzen 2002c). Thus, we released hatchlings at 1000 hours and did not re-enter the dispersal area until the experiment concluded on 16 August. We checked pitfall traps at 0700, 1300, and 1900 h each day by walking along the river side of the fence to minimize disturbance by the observer. For hatchlings that reached the fence, we recorded the time it took hatchlings to disperse (= dispersal time) and the distance between the closest spot on the fence for that hatchling's release point and the trap the hatchling was caught in (= dispersion along fence). We checked traps for 9 days after release at which point the recapture rates were very low (Fig. S2) and scored all hatchlings not recaptured as dead. Forty-seven percent (203/428)

of hatchlings were not recovered, which is comparable to dispersal mortality in other studies of aquatic turtles (discussed above). We released all recaptured hatchlings in the River after identification. This work adhered to ABS/ASAB guidelines for ethical treatment of animals and was approved by the Iowa State University Institutional Animal Care and Use Committee (5-17-8509-J).

Analysis

We ran all analyses with SAS software (version 9.4). All mixed models included clutch as a random effect. We evaluated random effects using likelihood-ratio tests. To examine how offspring size and release distance influenced survival during dispersal, we first ran a generalized linear mixed model with survival to fence as a binary dependent variable and body size, release distance, their interaction, and replicate as independent variables. Offspring mass and SCL were highly correlated ($r^2 = 0.76$; $P < 0.0001$); therefore, future analyses focused mainly on mass as the metric for offspring body size unless otherwise stated. The body size*release distance interaction was not significant and was removed from the final model. We chose to analyze survival with generalized linear mixed models instead of other methods because (1) the fate of every individual was considered known, (2) we could not determine when hatchlings perished, and (3) we wanted to account for clutch ID as a random effect. We also calculated average linear and quadratic selection gradients for offspring mass and SCL at each release distance with logistic regressions to quantify the relative importance of body size on survival (Janzen and Stern 1998). We ran independent analyses for mass and SCL because they were correlated. We detected no significant quadratic selection, so we removed quadratic terms from the final models.

We used general linear mixed models to assess the effects of offspring body size and release distance on dispersal time (time-to-fence in days) and dispersion along the fence (distance between the closest spot on the fence for a hatchling's release point and the trap the hatchling was caught in) as the dependent variables. Offspring mass, release distance, their interaction, and replicate were the independent variables. The offspring mass*release distance interaction was not significant in either analysis and was removed from the final models.

We also employed linear regression to assess if offspring dispersal ability was related to how far females nested from water naturally. We regressed the collective survival (%) of clutch mates released at 25, 62.5, and 100 m, as well as average offspring mass, on how far females oviposited from water. We ran all four regressions separately because independent variables were correlated. One female crossed two roads and nested much farther from water (185 m) than the rest (51.3 ± 5.61 m); therefore, we excluded her data from these regression analyses. These regressions were 1-tailed tests because our predicted effects were directional.

RESULTS

Incubating embryos experienced mean, minimum, and maximum nest temperatures ± SD on the order of 28.9°C ± 0.39, 23.2°C ± 0.29, and 34.8°C ± 1.04, respectively. These thermal conditions are similar to thermal conditions experienced by natural nests at this field site (range 26.3–34.1°C, Kolbe and Janzen 2001; range of means ~23.4–30.5°C, St. Juliana et al. 2004). During the 9-day dispersal period,

hatchlings experienced minimum daily air temperatures of 15.7°C ± 1.62 SD (range 13–18°C) and maximum daily air temperatures of 25.9°C ± 1.76 SD (range 23–28°C; data gathered from a weather station ~15 km away, www.ncdc.noaa.gov). The only precipitation occurred on the fourth and eighth days of dispersal, with 0.38 and 0.10 cm of rainfall, respectively.

Potential predators observed in the dispersal area included one opossum (*Didelphis virginiana*) and one hognose snake (*Heterodon nasicus*). However, we detected fresh tracks of coyotes (*Canis latrans*) and raccoons (*Procyon lotor*), and have previously noted striped skunks (*Mephitis mephitis*), red foxes (*Vulpes vulpes*), various raptors, American crows (*Corvus brachyrhynchos*), blue jays (*Cyanocitta cristata*), great blue herons (*Ardea herodias*), common egrets (*Ardea alba*), bullsnakes (*Pituophis catenifer*), blue racers (*Coluber constrictor*), and northern water snakes (*Nerodia sipedon*) nearby. We did not observe predator tracks or disturbance around collection pits, suggesting predators did not consume hatchlings captured in traps.

Average egg mass of clutches was positively correlated with average offspring mass at emergence from nests ($r = 0.91$, $P < 0.0001$), but neither variable was correlated with clutch size (egg mass, $r = 0.05$, $P = 0.8700$; offspring mass, $r = 0.11$, $P = 0.7289$). The overall average egg mass, offspring mass, SCL, and clutch size ± SD were 14.39 ± 1.67 g, 11.40 ± 1.32 g, 31.35 ± 1.59 mm, and 43 ± 14, respectively.

Offspring survival decreased with increasing release distances (Fig. 2A; Table 1). The generalized linear mixed model did not detect an effect of hatchling mass or an interaction of mass*release distance on survival (Table 1). Field studies should use >200

individuals for adequate power to detect selection (Hersch and Phillips 2004), yet we used 141–145 hatchlings per release distance. Thus, sample size at each release distance may have precluded the ability of the model to detect a mass*release distance interaction. However, selection gradient analyses revealed mass and release distance interactively affected survival (Table 2). Neither SCL nor body mass influenced offspring survival at 25 or 62.5 m, but longer and heavier offspring had higher survival than shorter and lighter offspring when initiating dispersal 100 m from the fence (Fig. 3; Table 2). To illustrate, hatchlings smaller than the mean averaged 2–3 times lower probability of survival than their larger counterparts at the greatest distance (Fig. 3). We found no evidence of quadratic selection on either SCL or mass for hatchlings dispersing from any distance (Table 2). Offspring from the northern replicates (47.5%) had lower survival than those from the southern replicates (57.9%; Table 1). Clutch ID did not explain a substantive amount of variation in offspring survival ($\chi^2 = 1.50$, $P = 0.1104$).

Dispersal time increased with release distance (Fig. 2B; Table 1). Offspring mass, its interaction with release distance, release replicate (Table 1), and clutch ($\chi^2 = 2.32$, $P = 0.3127$) did not explain a meaningful amount of variation in dispersal time.

Dispersion along the fence increased with release distance (Fig. 2C; Table 1). However, neither body mass nor its interaction with release distance affected dispersion (Table 1). Hatchlings from the northern release points (27.2 ± 2.04 m) dispersed more directly to the fence than those from the southern replicates (33.7 ± 1.95 m; Table 1). Clutch again was not an important predictor of variation in dispersion ($\chi^2 = 1.66$, $P = 0.4363$). Most hatchlings were caught in pitfalls along the center of the drift fence and no

hatchlings were caught in pitfalls along the terminal 25 m of either end of the fence (Fig. S3).

Females that produced offspring with higher survival when dispersing from 100 m constructed nests farther from water than females that produced offspring with lower survival when dispersing from 100 m (Fig. 4C; Table 1). The survival estimates of offspring dispersing from 25 and 62.5 m were not correlated with how far females oviposited from water (Fig. 4; Table 1). In addition, females that produced heavier offspring constructed nests farther from water than females that produced lighter offspring (Fig. 4D; Table 1).

DISCUSSION

Optimal maternal investment in offspring is often a balance of conflicting pressures. While some maternal investment tradeoffs are well studied (e.g., offspring size vs. clutch size), how offspring performance might affect pre-natal investment strategies is unknown. We found that larger hatchling turtles had higher survival during dispersal from long distances than did smaller offspring. Moreover, mothers that produced clutches that were better at dispersing long distances accordingly oviposited their clutches farther from water. These findings suggest mothers producing good dispersers maximize the benefits of reduced nest predation farther from water, whereas mothers producing poor dispersers nest closer to shore because their offspring are less capable of dispersing longer distances.

In our experiment, juveniles released farther from the drift fence experienced lower survival than those released closer to the fence. Increasing mortality with dispersal distance is often assumed for dispersing animals (Brooker et al. 1999; Refsnider and Janzen 2010; Bonte et al. 2011), but empirical evidence is lacking. Previous studies of freshwater turtles found no effect of increasing dispersal distance on offspring survival (*C. serpentina*, Congdon et al. 1999; *Chrysemys picta*, Paitz et al. 2007) or a minor effect opposite of predictions (61% survival from 35 m and 65% survival from 70 m, *C. serpentina*, Kolbe and Janzen 2001). We increased the variation in release distances compared to previous studies to encompass more of the natural range of dispersal distances that wild *C. serpentina* experience, which presumably enabled us to detect an effect of dispersal distance on survival. Nevertheless, animals that disperse farther are likely exposed to predators and unfavorable environments for longer durations, which may explain the higher mortality observed in our experiment (for similar discussion, see Janzen et al. 2007). In addition, evidence from studies of roughed grouse (*Bonasa umbellus*, Yoder 2004), snowshoe hares (*Lepus americanus*, Sievert and Keith 1985), and *C. serpentina* (Janzen 1995) support theoretical predictions (Lima 1998) that such prolonged movement elevates predation risk. However, to our knowledge, we provide the first empirical support for the assumption that increasing dispersal distance from nests reduces offspring survival in animal taxa.

We predicted larger neonates would have higher survival during dispersal than smaller neonates, and that this size effect would increase with longer dispersal distance. Body size did not affect survival of hatchlings dispersing short or intermediate distances

but, in line with predictions, larger hatchlings had higher survival than smaller hatchlings when dispersing the longest distance during our experimental release. Selection generally favors larger turtle offspring during dispersal in *C. serpentina* (Janzen 1993; but see Congdon et al. 1999; Kolbe and Janzen 2001), *C. picta* (Mitchell et al. 2013; Tucker 2000; Paitz et al. 2007), and *Trachemys scripta* (Tucker 2000; Janzen et al. 2000a, 2000b; Janzen et al. 2007; Mitchell et al. 2013; but see Filoramo and Janzen 2002). For some animals with optional dispersal, larger juveniles are more likely to disperse than smaller juveniles (reviewed in Bowler and Benton 2005), possibly because larger juveniles are better able to tolerate the energetic costs and/or predation risk associated with greater movement. In freshwater turtles, size-biased survival during dispersal may be underpinned by survival decreasing with time exposed on land (Janzen et al. 2007) and larger offspring dispersing faster (Janzen et al. 2000a, 2000b). Nevertheless, we provide novel evidence that offspring size effects on dispersal success can depend upon the distance offspring are born from suitable juvenile habitat. Such crucial interactions between offspring phenotype and nest-site choice should be prime targets of selection driving maternal investment strategies.

Juveniles released farther from the fence arrived at the fence later and dispersed less directly to the fence. We predicted larger hatchlings would disperse faster than smaller hatchlings, as found in other freshwater turtles (*C. picta*, Tucker 2000; Paitz et al. 2007; *T. scripta*, Janzen et al. 2000a, 2000b). However, we found no effect of body size on dispersal time. Despite the importance of body size on locomotor performance in hatchling *C. picta* and *T. scripta*, previous dispersal experiments with *C. serpentina* have

detected no effect of body size on dispersal time (Janzen 1993; Congdon et al. 1999; Kolbe and Janzen 2001). Thus, while important for emydids, the effect of body size on dispersal speed may not be ubiquitous across all turtles. Additionally, dispersal speed data were only attainable on hatchlings that survived to the fence (N = 225), and survival at the longest distance was size-biased (discussed above). Thus, the lower survival of smaller hatchlings dispersing from the longest distance may have inhibited our ability to examine how juvenile size might affect dispersal speed.

We considered all hatchlings that did not reach the fence within 8 days after release as dead. Dispersal to the fence was densest around the middle of the fence (most direct path) and tapered off towards the distal ends of the fence. Indeed, no hatchlings were caught in the terminal 25 m of the fence on either end. Thus, successful dispersal around the fence was unlikely. In addition, 96% of recaptures occurred within 4 days of release, suggesting successful dispersal transpired rapidly after release. Moreover, mortality increases the longer hatchlings are exposed on land (Janzen et al. 2007). Collectively, these results support our assumption that non-captured hatchlings likely perished. Although we did not observe mortality events, avian predation can be heavy on hatchling turtles during dispersal (Janzen et al. 2000b), and we observed raccoon, opossum, and coyote activity around the periphery of the dispersal area. In addition, dispersing turtles may dehydrate, with water loss increasing with time spent on land (Kolbe and Janzen 2002c). Because precipitation only occurred on the fourth and eighth days of release, dehydration might have been a source of mortality during our experiment. Larger hatchling *C. serpentina* have higher rates of evaporative water loss,

but should survive longer on land because of greater absolute water content compared to smaller individuals (Finkler 2001). Thus, our finding that selection favored larger hatchlings when dispersing from the longest release distance further suggests dehydration, in addition to predation, as a source of mortality in our study.

Turtle nests constructed farther from environmental edges often experience a reduced likelihood of predation (Kolbe and Janzen 2002a; Marchand and Litvaitis 2004; Strickland et al. 2010). However, for embryos that successfully hatch, neonates must then emerge from the nests and disperse to water. Thus, maternal investment should evince a tradeoff between maximizing nest survival farther from water and reducing dispersal distance closer to shore. As discussed above, larger hatchlings had higher survival than smaller hatchlings during dispersal from the longest distance in our experiment. Therefore, mothers producing these bigger and better dispersing offspring should construct nests farther from water because their offspring are more capable of dispersing longer distances to water upon emergence. As predicted, mothers that produced heavier offspring and offspring that were better dispersers at long distances constructed nests farther from water than mothers that produced lighter offspring and offspring that were poorer dispersers at long distances. Nesting closer to shore elevates predation risk for embryos in the nest, but if smaller offspring successfully hatch, they need to be close enough to shore to have a reasonable probability of surviving dispersal to water.

These results suggest maternal investment strategy can indeed be sensitive to offspring phenotype. Diamondback terrapin (*Malaclemys terrapin*) that produce larger eggs nest in warmer locations than mothers that produce smaller eggs, and warmer nests

are more likely to produce female offspring (Roosenburg 1996). If female offspring benefit more from hatching from larger eggs than male offspring, then such covariation between nest-site choice and offspring size would be adaptive (see also Morjan and Janzen 2003). However, few studies have tested for adaptive nest-site choice dependent upon offspring phenotype. Studies of a lizard (*Bassiana duperreyi*, Shine et al. 1997) and a turtle (*C. picta*, Mitchell et al. 2013) cross-fostered eggs between nests to examine if mothers chose nest sites that were tailored for their offsprings' phenotypes. However, both studies found that mothers chose nest sites that were equally beneficial for unrelated offspring as they were for their own offspring. In contrast, offspring growth of a fly (*Liriomyza sativae*, Via 1986) and a butterfly (*Euphydryas editha*, Singer et al. 1988) on specific host plants increased with female preference for that host plant. Although these studies suggest oviposition choice can covary with offspring traits, the fitness consequences in these systems are unclear. We provide a robust demonstration that nest-site choice covaries with offspring phenotype in *C. serpentina*, and that such variation maximizes offspring survival and, thus, maternal fitness.

Turtles, like most organisms, select oviposition sites without observing offspring performance capabilities. Thus, how could mothers "know" the abilities of their offspring so as to tailor investment for their phenotype? Such prenatal investment depending upon offspring phenotype may be possible via a positive genetic covariance between size of offspring produced and how far mothers nest from water. For example, genetic covariation is thought to maintain the association of increased offspring growth on certain host plants with maternal preference for ovipositing on those plants in *L. sativae* (Via

1986) and *E. editha* (Singer et al. 1988), as discussed above. Alternatively, variation in maternal age might drive much of the variation in investment strategy in turtles. *Chelydra serpentina* grow indeterminately throughout their lives, and larger turtles produce heavier eggs (Congdon et al. 2013; Armstrong et al. 2017; Hedrick et al. 2018). Thus, young mothers may nest closer to shore because they produce smaller offspring, but may nest farther from water as they produce larger offspring later in life. Similarly, *C. picta* produce heavier eggs and nest farther from water with age (Harms et al. 2005). However, increasing predation risk to adult females the farther they travel from water could drive such age-specific variation in nest-site choice (Harms et al. 2005; Paitz et al. 2007; but see Refsnider et al. 2015). Younger mothers may nest closer to shore to maximize their own survival, whereas older females may tolerate greater risk to themselves because they have fewer future reproductive opportunities (i.e., terminal investment hypothesis, Williams 1966) or may have lower risk because of their larger body size (Tucker et al. 1999). Optimal maternal investment in aquatic turtles, as perhaps in all oviparous taxa, may then be shaped by a complex interaction of risk to the mother, risk to the nest, and offspring dispersal ability.

Our findings suggest offspring phenotype influences nesting strategy. However, interpretation of causation is limited because our test of the offspring phenotype-nest site covariation was correlative and not experimental. Thus, an alternative explanation could be that mothers invest in egg size (and thus indirectly in offspring dispersal ability) depending on how far they will nest from water (i.e., anticipatory maternal effect; Marshall and Uller 2007; Kotrschal et al. 2012). However, this interpretation is unlikely

because egg size increases with maternal size (as discussed above) and offspring benefit from larger egg size in more aspects than just enhanced dispersal ability (increased hatching success, reduced predation risk during early aquatic life, improved competitive ability, etc.; Froese and Burghardt 1974; Janzen and Warner 2009). Thus, as they age, mothers probably produce larger offspring to maximize multiple aspects of early-life success, including dispersal ability, which frees them to nest farther from shore to lower predation risk of nests.

Maternal investment tradeoffs are shaped by environmental context and intrinsic female traits. However, optimal investment may also vary by offspring phenotype. Yet few studies have assessed the role of offspring phenotype on nesting strategy and none have shown how such covariation affects maternal fitness. We provide the first evidence for the assumption that increasing dispersal distance from nests to post-natal habitat elevates offspring mortality in animal taxa. This effect was also size-dependent, such that smaller offspring were more severely affected by increasing dispersal distances. Moreover, females that produced larger and better dispersing offspring constructed nests farther from water than females that produced smaller and poorer dispersing offspring. Thus, females that produced better dispersing offspring maximized the benefits of lower nest predation farther from water, whereas females producing poorer dispersing offspring presumably were constrained to nest closer to water so their offspring would have a reasonable chance of dispersing successfully if they hatched. Collectively, these findings elucidate the sensitivity of female investment in offspring phenotype and identify that covariation between nest-site choice and offspring phenotype maximizes offspring

survival and maternal fitness. Further considering the role of offspring performance on maternal behavior will shed light on this underexplored influence of pre-natal investment strategies.

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FIGURE LEGENDS

Fig. 1. (A) Predicted dispersal success of hatchling turtles as a function of the interaction between hatchling body size and how far nests are laid from water. (B) Generalization of nest success (i.e., not depredated) increasing with distance to water. We predict optimal nest-site placement is a tradeoff between nest success increasing farther from water with offspring dispersal success decreasing farther from water. However, we also predict larger offspring will be less affected by increasing dispersal distances compared to smaller offspring. Thus, optimal distance from water for turtle nests should reside where the surfaces of panels A and B intersect. Panel A is a hypothetical surface based on our predictions, whereas panel B is a generalized surface based on previous work (Kolbe and Janzen 2002a; Marchand and Litvaitis 2004; Strickland et al. 2010).

Fig. 2. Effects of dispersal distance on A) survival, B) time to fence, and C) dispersion along the fence of hatchling *Chelydra serpentina* during experimental dispersal. Data are plotted as least squares means with standard errors. Statistical results are reported in Table 1.

Fig. 3. Effects of standardized straight carapace length and mass on the probability of survival for hatchling *Chelydra serpentina* as they dispersed from "nests" (A) 25 m, (B) 62.5 m, and (C) 100 m to a drift fence. Probability of survival was estimated using cubic splines, and dashed lines represent standard errors (Schluter 1988). Open circles along the

top and bottom axes represent individual hatchlings. Statistical results are reported in Table 2.

Fig. 4. Relationships between the distance female *Chelydra serpentina* oviposited from water and the survival of offspring dispersing from A) 25 m, B) 62.5 m, and C) 100 m, and D) average offspring mass. Statistical results reported in Table 1.

Table 1. Statistical results of models of survival and dispersal of hatchling *Chelydra serpentina*. * denote independent terms that were not significant and were removed from the final models. For models with the dependent variable 'nest distance to water', all independent terms were regressed separately because independent variables were correlated with each other.

Dependent variable	Independent variable	r	df	Test Statistic	*P*
Survival	Mass		1, 409	$F = 1.46$	0.2276
	Release Distance		2, 409	$F = 44.69$	<0.0001
	Replicate		1, 409	$F = 5.56$	0.0189
	Mass x Release Distance*		2, 407	$F = 1.80$	0.1662
Time to Disperse	Mass		1, 206	$F = 3.49$	0.0632
	Release Distance		2, 206	$F = 30.81$	<0.0001
	Replicate		1, 206	$F = 1.66$	0.1991
	Mass x Release Distance*		2, 204	$F = 1.48$	0.2291
Dispersion Along Fence	Mass		1, 206	$F = 0.28$	0.5977
	Release Distance		2, 206	$F = 32.51$	<0.0001
	Replicate		1, 206	$F = 7.62$	0.0063
	Mass x Release Distance*		2, 204	$F = 0.01$	0.9940
Nest Distance to Water	Average Offspring Mass	0.6023	13	$t = 2.61$	0.0113
	Offspring Survival at 25 m	0.0100	13	$t = 0.04$	0.4845
	Offspring Survival at 62.5 m	0.0900	13	$t = -0.31$	0.5000
	Offspring Survival at 100 m	0.4806	13	$t = 1.90$	0.0410

Table 2. Standardized average selection gradients quantifying the linear (β) and quadratic (γ) effects of straight carapace length (SCL) and mass on the survival of hatchling *Chelydra serpentina* during experimental dispersal. Significant effects are bolded.

Release Distance	*n*	Variable	Standard Deviation		Average Selection Gradient	SE	Chi-square	*P*
25	145	SCL	1.62	β	-0.0134	0.0305	0.1933	0.6602
25	145	SCL	1.62	γ	0.0288	0.7436	0.0015	0.9691
25	145	Mass	1.35	β	-0.0023	0.0313	0.0054	0.9413
25	145	Mass	1.35	γ	0.2457	0.2894	0.7212	0.3957
62.5	142	SCL	1.51	β	0.0519	0.1019	0.2590	0.6108
62.5	142	SCL	1.51	γ	0.8640	2.6892	0.1032	0.7480
62.5	142	Mass	1.32	β	-0.0264	0.1013	0.0679	0.7945
62.5	142	Mass	1.32	γ	0.4631	1.0993	0.1775	0.6735
100	141	SCL	1.61	β	0.4299	0.1656	6.7357	**0.0095**
100	141	SCL	1.61	γ	-5.4800	6.5992	0.6896	0.4063
100	141	Mass	1.35	β	0.3187	0.1489	4.5826	**0.0323**
100	141	Mass	1.35	γ	-3.2915	2.1866	2.2659	0.1322

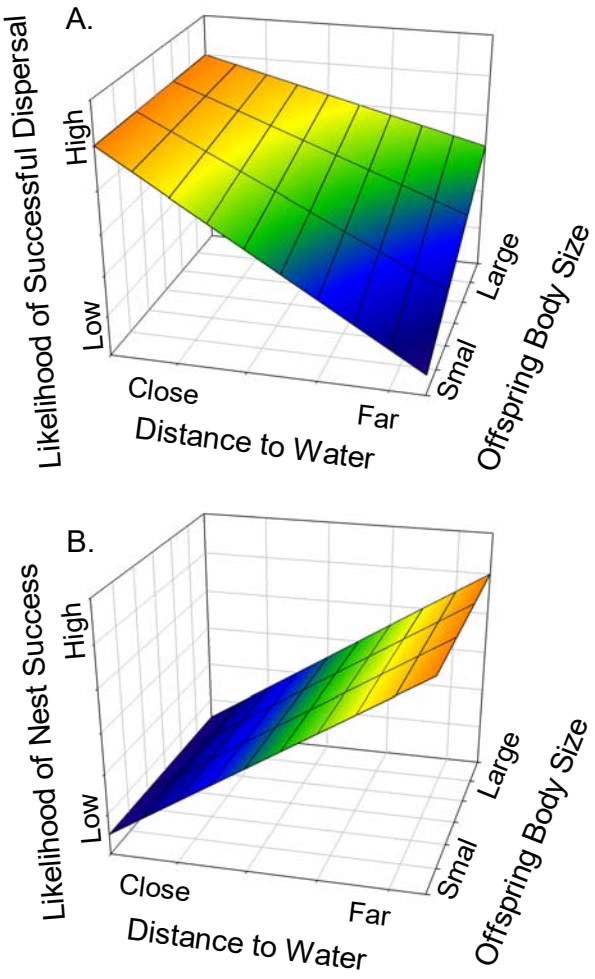
A.
Likelihood of Successful Dispersal
High
Low
Close
Distance to Water
Far
Smal
Large
Offspring Body Size
B.
Likelihood of Nest Success
High
Low
Close
Distance to Water
Far
Smal
Large
Offspring Body Size

Figure 1.

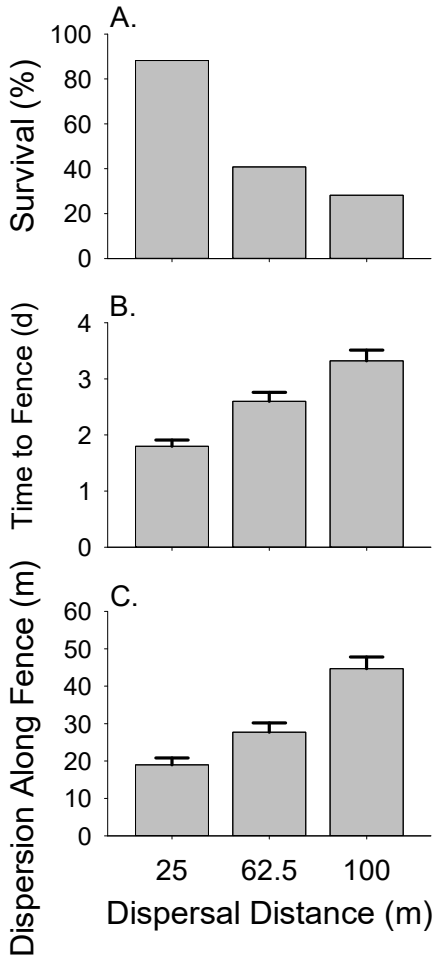
A.
Survival (%)
100
80
60
40
20
0
B.
Time to Fence (d)
4
3
2
1
0
C.
Dispersion Along Fence (m)
60
50
40
30
20
10
0
25
62.5
100
Dispersal Distance (m)

Figure 2.

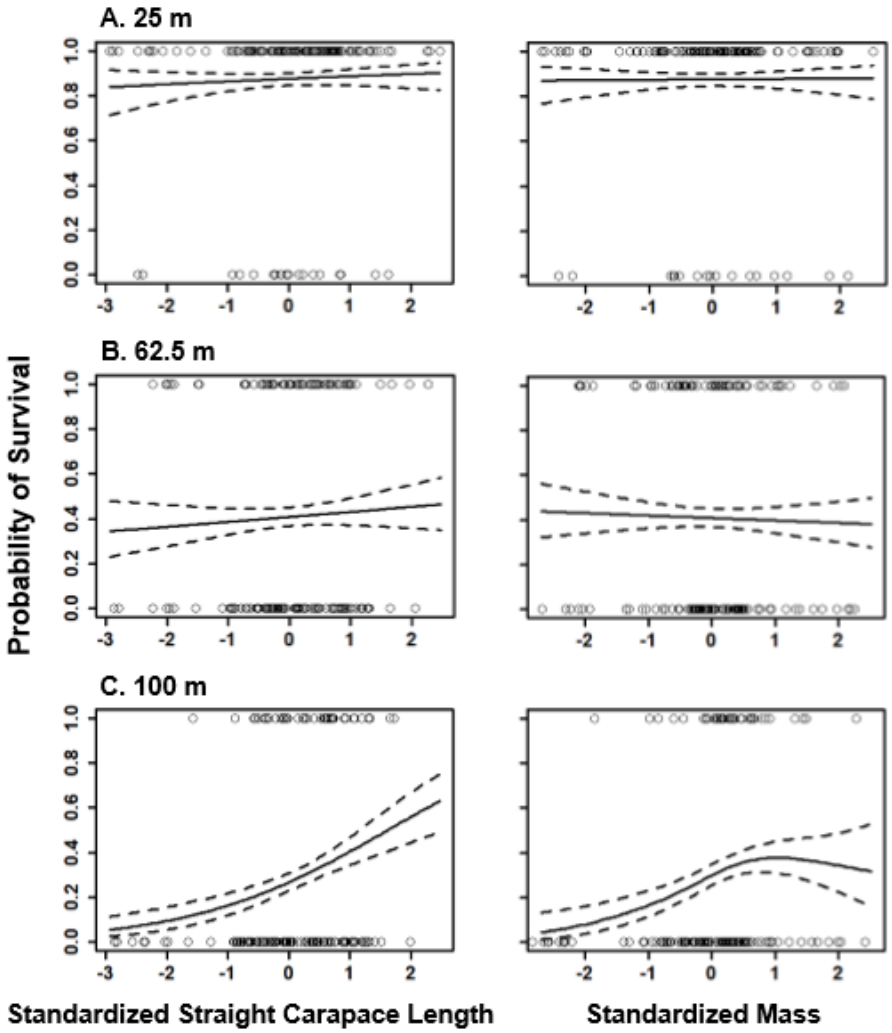
A. 25 m
B. 62.5 m
C. 100 m
Probability of Survival
0.0
0.2
0.4
0.6
0.8
1.0
-3
-2
-1
0
1
2
Standardized Straight Carapace Length
Standardized Mass

Figure 3.

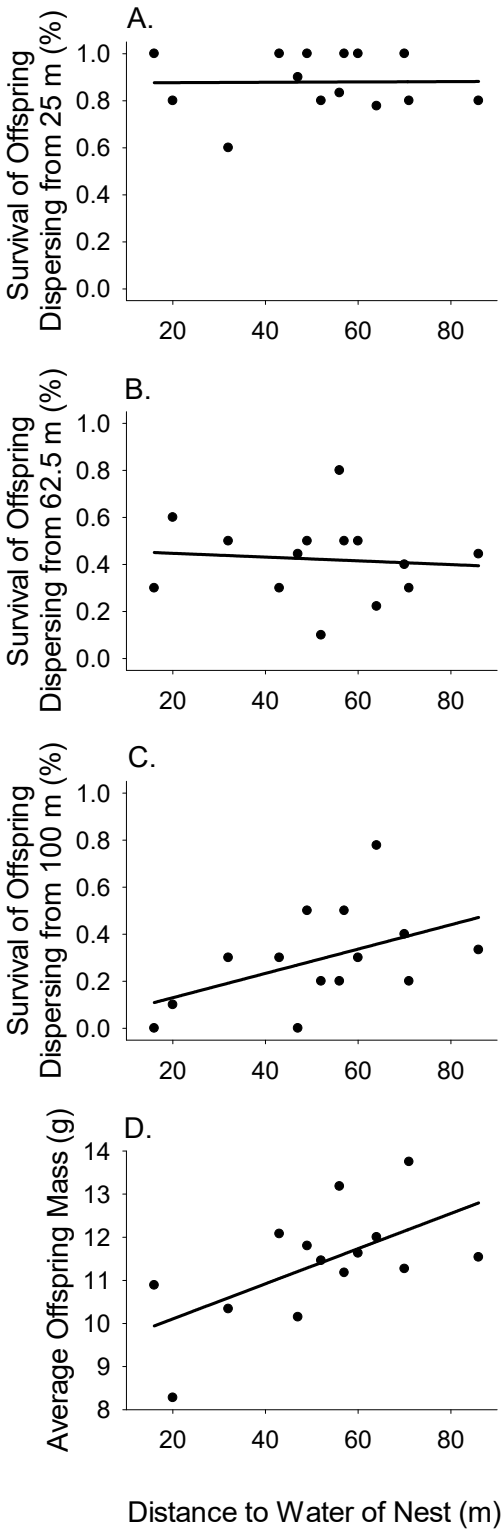
A.
Survival of Offspring Dispersing from 25 m (%)
B.
Survival of Offspring Dispersing from 62.5 m (%)
C.
Survival of Offspring Dispersing from 100 m (%)
D.
Average Offspring Mass (g)
Distance to Water of Nest (m)

Figure 4.

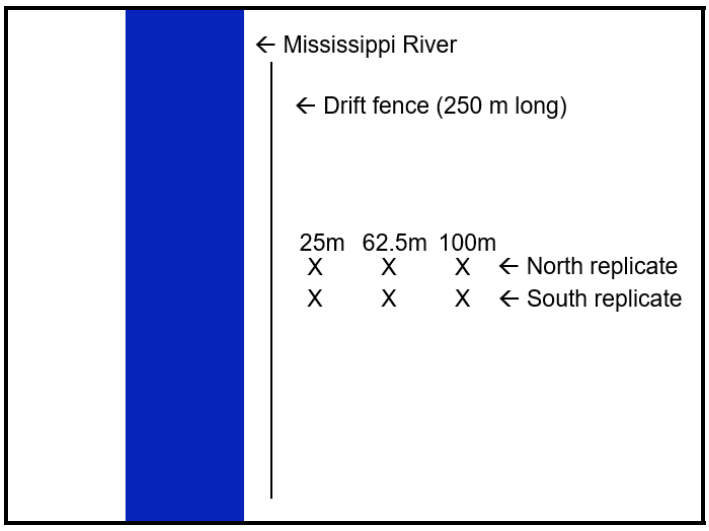

Figure S1. Schematic of experimental drift fence design. Xs denote locations where hatchling *Chelydra serpentina* were released.

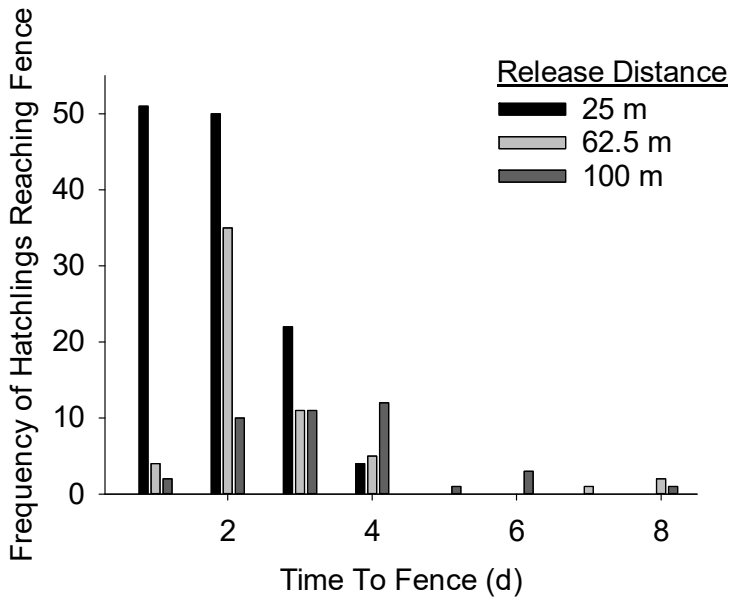

Figure S2. Effect of release distance on the time required for hatchling *Chelydra serpentina* to reach the fence during experimental dispersal. Statistical results are reported in table 1.

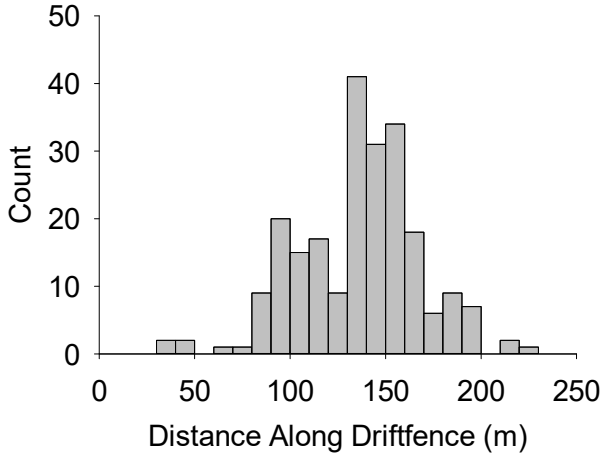

Figure S3. Distribution of locations that hatchling *Chelydra serpentina* were recaptured along a 250 m drift fence during experimental dispersal. Pitfall traps were spaced every 5 m along the fence and bin width is 10 m.